

NOTES ON *PIERIS NAPI* (L.) SSP. *THOMSONI* (WARREN)
AB. *FASCIATA* (MULLER AND KAUTZ) AND F. *FLAVA* (KANE)
(GREEN VEINED WHITE)

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Abstract

Breeding experiments with *Pieris napi thomsoni* have shown the genetic basis behind both the pattern variation ab. *fasciata* and the ground colour variation f. *flava*. The possible ecological roles of both variations in wild populations are discussed. These may involve both thermoregulation and visual signalling in the ultraviolet range.

Introduction

From early in the 20th century up to the end of the 1950s livestock and adult specimens of various aberrations of *Pieris napi* were widely sold by dealers. A few entomologists became very interested in their genetics and reared carefully segregated broods. Some of the resulting information was published, but other questions remained unanswered.

The following describes some recent breeding experiments by the author with the abs. *fasciata* and *flava*. The results allow some conclusions to be drawn about both their inheritance and possible value to wild populations.

Descriptions of aberrations and forms

ab. *fasciata* (Plate: A. Figs: 2, 4-10):

In the female this ranges from specimens showing a light dusting of scales between the two forewings discal spots through to the most extreme form in which heavy, dark scaling joins the discal spots and also runs up to the third, supradiscal, spot (usually masked by the apical blotch). Sometimes one or more median spots may develop on the upperside of the hindwings. The male shows a similar, but much weaker, tendency on the forewings. Male hindwings always remain typical.

Aberration *fasciata* probably occurs from time to time in most populations of *napi* in the British Isles. In the Scottish subspecies *thomsoni* and the Irish subspecies *britannica* (Muller and Kautz) minor forms are not uncommon (e.g. Plate: A. Fig. 1) and could be considered as part of the range of the typical form (Greer, 1922-23).

It could be argued that while *fasciata* is defined as an 'aberration' in England and Wales (an aberration being a colour or pattern variation that occurs uncommonly and unpredictably in wild populations) it may become a 'form' in parts of Scotland and often Ireland (a form being a colour or pattern variation that regularly occupies a significant proportion of the population/s of a species within a defined geographical region).

Form *flava* (Plate A. Figs: 2-6)

This very variable form is only expressed in the female, the male always appearing typical. The female's ground colour is replaced by any of a range of tones, from one

practically indistinguishable from white, through shades of buff to strong ochreous-yellow. While *flava* usually affects the whole of the female upper surface some specimens exhibit just a flush of colour in the cell area of the forewings.

On the underside of the female the yellow-orange colouration of the hind wing and forewing tip is usually intensified but, except in rare, extreme examples (Plate: A Fig: 4), the discal area of the forewing remains white.

Form *flava* does not occur in the English subspecies *sabellica* (Stephens), but occupies varying proportions of many Scottish and Irish populations. Thomson (1970) states that in Scotland it becomes more frequent the further north one travels.

It also occurs in the Scandinavian subspecies *adalwinda* (Fruhstorfer) in which subspecies the intensity of the *flava* colouration increases northwards (V. B. Meyer-Rochow, pers. comm.). Tolman (1997) states that in sub-arctic Scandinavia *flava* is only present in montane regions. It also occurs in the closely related species *P. bryoniae* (Ochs.)

History in captivity

While many entomologists have come across both *fasciata* and *flava* these forms have been bred intensively by only a few. The famous Lepidoptera dealers H. W. Head and the two Newmans, L. W. and L. H., maintained stock of various forms of *napi* for many years. These originated mainly from Ireland (Donegal) although the Newmans sometimes sold strains from Northern Scotland (Caithness). The most famous (Irish) strains showed *fasciata* on typical ground colour and also on the yellow ground colour of the very rare recessive aberration *sulphurea* Schoyen (illustrations in Russwurm, 1978). The *sulphurea* strain originated from a wild female aberration sent to Head by a school mistress in Tullybeg, Co. Donegal in 1909 (Head, 1939). It is genetically separate from *flava*. The Newmans also added an albino strain into the mix, ab. *pallidus* (Frohawk).

J. A. Thompson, who specialised in aberrations of the Pieridae, reared all these forms, and others, through many carefully segregated broods in the 1940s and 1950s and crossed them with *flava* from Scotland (Thompson 1947 and 1954, Newman, 1954).

S. R. Bowden bred both *napi* and *bryoniae* in large numbers (often in collaboration with N. T. Easton). His focus was the complex taxonomy surrounding *napi*, *bryoniae* and their many races. In the course of his work he was familiar with both *fasciata* and *flava* (Bowden, 1956 and 1979).

Previous remarks on genetics

J. A. Thompson's intention was to publish a complete guide to the genetic basis of all the pattern and colour variation in the species. However he was unable to finish this work and published only preliminary notes. He said (Thompson, 1954) that *flava* is a sex-limited form (i.e. it is carried by both sexes, but expressed only in one – the female). However he shed no light on whether it might be caused by one, or multiple, genes. As regards *fasciata* he stated (Thompson, 1947) that while it was previously assumed to be caused by a single recessive gene his own work had

indicated what he called 'a cumulative gene' (i.e. a multifactorial form in which many genes act together with cumulative effect). He proposed (though no supporting data was given) separate genetic control for the *fasciata* character on the upper and under surfaces, and also between the sexes. For this reason he gave separate names to this aberration on either surface of the male butterfly (*fulgoris* for the upperside and *lachrymosa* for the underside) leaving *fasciata* to apply only to the female upperside. He said he was still working on the inheritance of banding on the female underside. Thompson's specimens are now in the Natural History Museum, London but unfortunately there are no explanatory notes with them, nor have any note books or other detailed records of his work reached the museum.

I have been unable to trace any publications by S. R. Bowden on the genetics of *fasciata*. In one paper (Bowden, 1956) he describes *flava* as a 'cumulative' (multifactorial) form. However, later (Bowden, 1979) he references work by Lorkovic which suggests that the equivalent form in the closely related species *bryoniae* may be caused by a dominant gene affected by modifiers.

Recent breeding experiments

I have conducted breeding experiments with two separate, Scottish strains of *P. napi*.

The first began with a wild female *napi* captured in August 1997 on Barra in the Outer Hebrides. She showed typical white ground colour and was transitional to *fasciata* on the forewings (Plate: A. Fig: 1). A total of about 450 specimens were reared over four successive broods. In each brood one pair of specimens were mated to give rise to the next generation with selection taking place for the strength of expression of the *fasciata* character only. Generation F1 produced largely typical butterflies as regards *fasciata*, with just one female being a weak form of the aberration. She was also a very pale form of *flava* and was paired with a male showing a larger than usual forewing discal spot. The specimens in each brood, from F2 to F4, formed a smooth gradient from typical to *fasciata*. But the percentage (and intensity) of *fasciata* in each brood increased while the proportion of typical specimens fell. The most heavily marked *fasciata* is illustrated (Plate: A. Fig: 2).

As regards *flava* a number of other females in the F1 were pale *flava* but it was not possible to work out the percentage of these because the form seemed to grade imperceptibly into type. Form *flava* occurred in a percentage of the F2 (including the female used for breeding) and all female specimens in the F3 and F4 generations were *flava* of fairly consistent intensity (Plate : A. Fig. 2). In an additional out-cross experiment several female specimens from the F1 brood that appeared to show typical ground colour were paired with typical males from stock originating in Sussex. About 100 adults were reared. A proportion of the females in this brood (again impossible to quantify) were *flava*. Some of these were a little more intensely coloured than any *flava* reared in the pure Outer Hebrides strain (Plate: A. Fig: 3).

The second strain began, in August 2000, with a wild, white female from Orkney which was a lightly marked *fasciata*. Six successive broods were reared, totalling approximately 2,550 specimens. As with the Barra strain, selection was only for

specimens showing increasingly strong development of *fasciata* and not specifically for *flava*. The results, as regards *fasciata*, were similar to the Barra experiment except that the Orkney strain produced more extreme forms (Colour plate: A. Figs: 6-10). Form *flava* appeared once again in the F1 brood. Up to ten specimens were used as parents for each brood and I always included some *flava* females among these. Form *flava* females made up a proportion of every subsequent generation. Their colour varied from those virtually indistinguishable from type through to strongly yellow specimens (Plate: A. Fig. 5). A very pale form is shown in Fig. 6. A few females showed *flava* colouration replacing white on the underside of the forewings (Fig. 4).

Inheritance of *fasciata*

Ab. fasciata is inherited as a multifactorial form, as Thompson stated. However I've seen no clear evidence to support his suggestion that the *fasciata* character is the result of different genes on upper and under surfaces and between the sexes. The female black markings in typical, and *fasciata*, specimens are always heavier on the upperside than the underside and the reverse applies in the male. My strains showed a smooth gradation in the female from specimens showing light *fasciata* only on the upperside right through those showing it heavily on both surfaces. The reverse situation applied to the male. This is consistent with a multifactorial form in which the penetrance (or degree of expression) of the genes is affected by modifier genes of differing 'strength' on

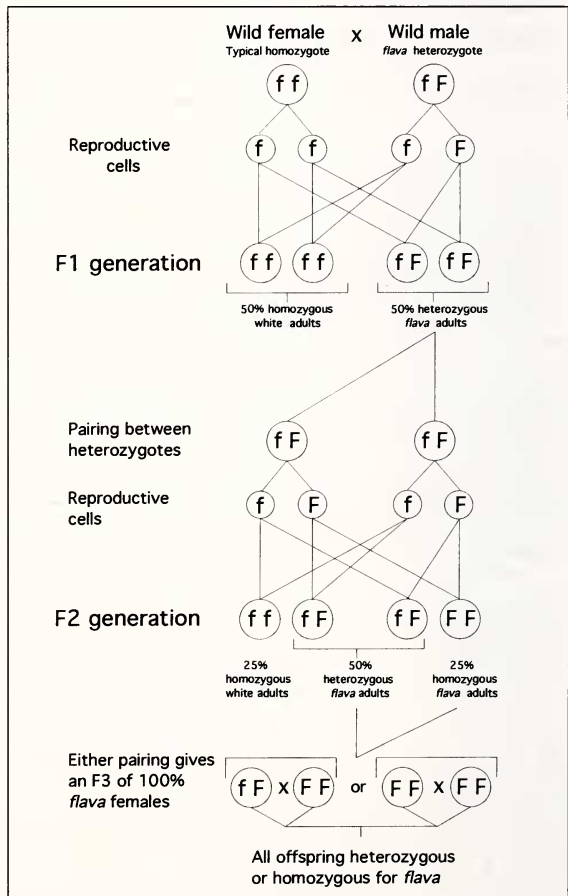


Fig. 1. Inheritance in *Pieris napi* (L.)

F = *flava* gene f = white ground colour gene

either surface and between the sexes. It does not seem to demand an explanation involving separate genetic systems between the different surfaces and sexes.

The great variability of form *flava* leads to broods in which female specimens seem to grade from those with typical white ground-colour, through varying pale shades of *flava* to strongly buff-yellow specimens. Superficially this is a pattern typical of multifactorial inheritance. However the results of these experiments actually indicate a dominant gene, the expression of which is very variable due to the action of a series of modifier genes.

The F3 and F4 generations from the Barra strain were 100% *flava* and the genetics diagram (Fig. 1) shows how that could have been achieved, assuming dominance for the *flava* gene. It also assumes that the original female was type and the male carried the *flava* gene, although the reverse situation would give the same results.

If *flava* is controlled by a multifactorial complex it is very unlikely that a pure strain could have been established so quickly. To demonstrate why, we need look no further than the results for *fasciata*, in which typical specimens continued to appear in the final, F6 generation, of the Orkney strain. Further evidence for *flava* being dominant comes from the cross of typical white Barra females with typical Sussex males, which gave rise to specimens of *flava* in the F1. Form *flava* is unknown in Southern England so at least one of the apparently typical Barra females must have carried the *flava* gene and its immediate appearance in the F1 strongly suggests dominant inheritance. The fact that the *flava* carrying female appeared to be a typical white example shows that the expression of *flava* is so variable that at one extreme it is indistinguishable from the typical form.

Ecological significance of variable dark markings

Both Bowden (1979) and Majerus (1998) discuss the thermoregulatory role of dark wing scaling in allowing adult butterflies to absorb heat through the wing surface. A range of northern, or montane, species or subspecies are cited which show more profuse dark scaling than southern counterparts. Experiments with some have shown that the dark scaling allows them to heat up more rapidly – a distinct advantage in a cooler and cloudier environment. While such experiments have not been conducted with *napi* it is clear that the darkest races occur in northern climes and the female of the closely related montane species *bryoniae* is heavily melanic.

Possible ecological significance of *flava* colouration

The two most likely explanations for the increasing proportion of *flava* in Northern European *napi* are discussed below.

Thermoregulation

Bowden (1979) discusses the possibility that the ochreous/yellow pigmentation of *flava* may absorb more heat than typical white pigmentation, although this is based on work with other species, not with *napi*. The increasing proportion of *flava* as one

moves north supports this idea. I have found no information on whether *flava* increases in intensity as one moves northwards in Scotland but, as mentioned earlier, Meyer-Rochow states that this is the case in Scandinavia.

Ultraviolet reflectance

Some butterflies, notably some Pieridae, have ultraviolet (UV) patterns on their wings, or a general UV fluorescence, visible to them but not to us. When photographed on black and white film using a lens filter which lets through only UV light, this hidden colour is revealed. The pattern, or fluorescence, is often gender-specific and plays a role in communication between the sexes and even between species (Silberglied, 1973). Male *napi* never carry UV patterns or fluorescence, nor do English females. However *flava* females do fluoresce under UV (Bowden, 1977). The accompanying black and white UV photograph shows *napi* from my Orkney stock (Plate C). Plate B shows the same specimens photographed under normal conditions. This photograph, albeit illustrating a small sample, shows increasing intensity of UV reflectance with increasing intensity of *flava* colouration. Figure 2 has just a very light flush of *flava* colour in the forewing 'cell' area and reflects very little UV. Figures 3 and 4 are increasingly strong expressions of *flava* and show increasingly strong UV reflectance. Even Fig 6, which is a rare form showing *flava* on the underside of the forewings (also illustrated on Plate A. Fig 4.), shows a slight reflection in this area while the typical white underside in Fig 5 does not. However Bowden found that the correlation between the intensity of *flava* coloration and the intensity of UV reflectance was not always exact in the closely related species *bryoniae*. Meyer-Rochow (1997) stated that in *napi* ssp. *adalwinda* in Finland the intensity of UV reflectance of females increases consistently as one travels north into the Arctic Circle. He says (pers. comm.) that most, but not all, of the females that reflected UV were *flava* but suggests there was a broad correlation between intensity of UV reflectance and intensity of *flava*. In light of the extreme variability of *flava* it's possible that the typical females that he found to be UV-reflective may have been genetically *flava* and contained just enough *flava* pigment to reflect UV. The value of the UV reflectance of *flava* would probably be that in northern regions, where low temperatures and lack of sun will often keep butterflies grounded, there is likely to be an advantage in their being as visible to each other as possible during brief spells of flight.

Supporting evidence, from its local distribution, for both thermoregulatory and ultraviolet communication roles for *flava*.

Lorimer (1983) states that Orkney *napi* from moorland, as opposed to those from low lying marshland, are often very yellow-tinted. In other words, even within a small geographical region *flava* is apparently more intensely coloured in those areas likely to experience less sunlight and lower temperatures.

Thomson (1970) says that in the wild, *flava* is more frequently seen in the first brood in Scotland than in the second, summer, brood. It is therefore commonest in

the brood in which adults would experience less sunlight and lower temperatures. He adds that even within a single, wild, brood females with visible *flava* coloration tend to emerge earlier than typical white ones (therefore, at least in the case of the spring brood, *flava* would, once again, be most common when cloud cover is likely to be greater and temperatures lower).

These observations support the suggestions of both a heat-absorbing advantage of *flava* and the advantage of increased UV reflectance. Both factors would give a *flava* female some advantage over a typical white one in upland areas, in the early part of the spring brood and in the spring, as opposed to the summer brood.

Possible environmental role in the expression of *flava*

Flava seems to be a genetic dominant to type so one would expect that if *flava* females, or males carrying the gene, are frequent in the spring brood then they should be plentiful in the summer brood too. But Thomson's observations that *flava* is more abundant in the spring brood contradicts this. However, as discussed earlier, the expression of *flava* is so variable that what appear to be typical white females can actually be *flava* carriers. So the discrepancy that Thomson reports could be explained if some unknown environmental condition plays a role in controlling the expression *flava*, such that a high proportion of female *flava* carriers of the summer brood do not express the gene in their wing colour. In light of the discussion above it is possible that *flava* may be of no benefit to a butterfly in the warmer and sunnier conditions of the summer brood. It might even be deleterious through the danger of over-heating, or because the increased visibility of females may attract the time-wasting attentions of male butterflies during the short period of her life when a mated female is searching for foodplant on which to lay eggs.

Detailed breeding work, under controlled conditions, would be necessary to investigate further an environmental role in the expression of *flava*.

Aknowledgements

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Plate A

- | | |
|---|---|
| 1 | 2 |
| female transitional to ab. <i>fasciata</i>
Captured Barra, Outer Hebrides, July 1997 | female <i>flava</i> + <i>fasciata</i>
Bred Barra, F4, July 1998 |
| 3 | 4 |
| female <i>flava</i>
Bred Barra x Sussex F1 | female <i>flava</i> + <i>fasciata</i>
Bred, Orkney, F3, July 2001 |
| 5 | 6 |
| female <i>flava</i> + <i>fasciata</i>
Bred Orkney, F3, July 2001 | female <i>flava</i> + <i>fasciata</i>
Bred Orkney, F6, August 2002 |
| 7 | 8 |
| male <i>fasciata</i>
Bred Orkney, F6, August 2002 | male <i>fasciata</i>
Bred Orkney, F6, September 2002 |
| 9 | 10 |
| female <i>fasciata</i>
Bred Orkney, F6, August 2002 | female <i>fasciata</i>
bred Orkney, F6, August 2002 |

Plate B

- | | |
|---|---|
| 1 | 2 |
| female, typical white ground colour
Bred Orkney, F3, July 2001 | female, very pale <i>flava</i>
(similar to Fig. 6 on colour plate)
Bred Orkney, F4, April 2002 |
| 3 | 4 |
| female, average intensity of <i>flava</i>
(similar to Fig. 2 on colour plate)
Bred Orkney, F1, April 2001 | female intense <i>flava</i>
(similar to Fig. 5 on colour plate)
bred Orkney, F3, July 2001 |
| 5 | 6 |
| female, typical white ground colour
Bred Orkney, F6, August 2002 | female showing <i>flava</i> on
forewing underside (this is Fig. 4 of colour plate)
Bred Orkney, F3, July 2002 |

Plate C

Specimens on Plate B photographed in sunlight using an ultraviolet filter



Plate A

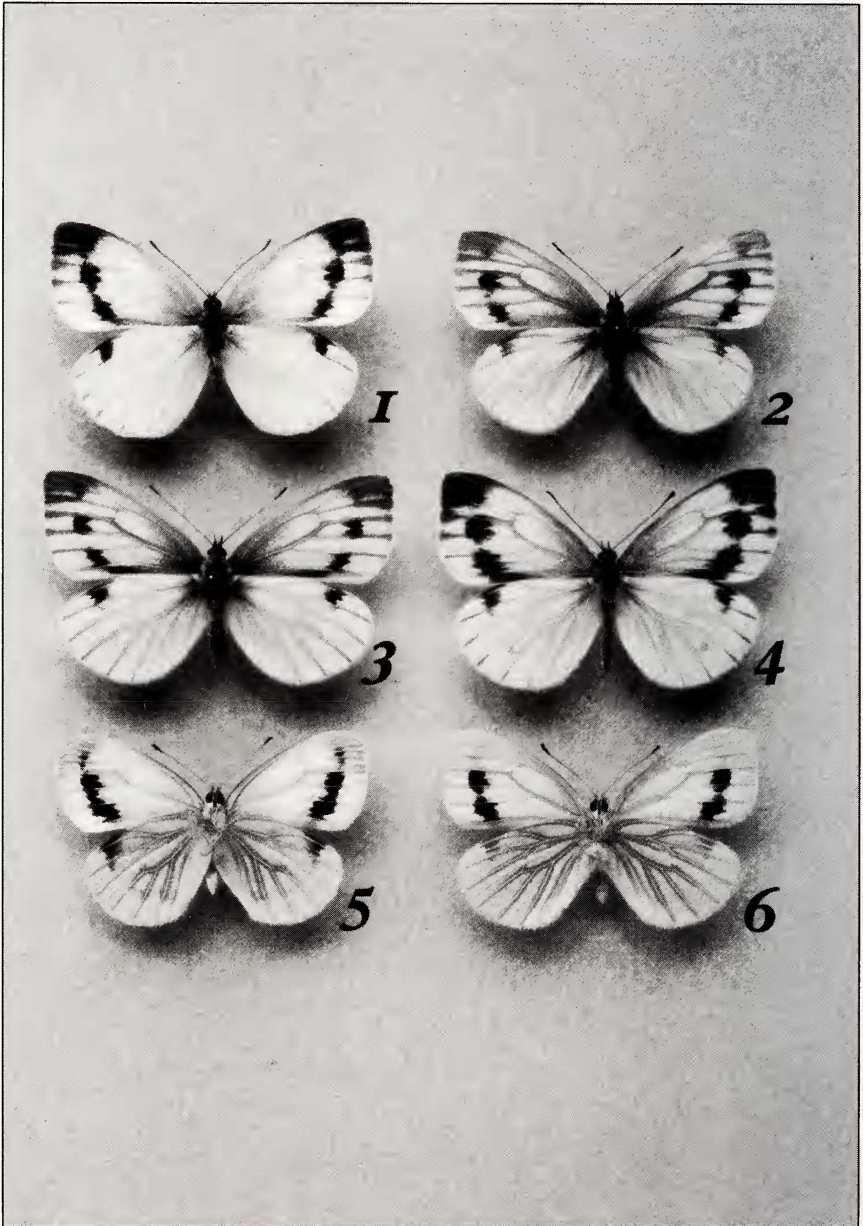


Plate B

(see page 58 for captions)

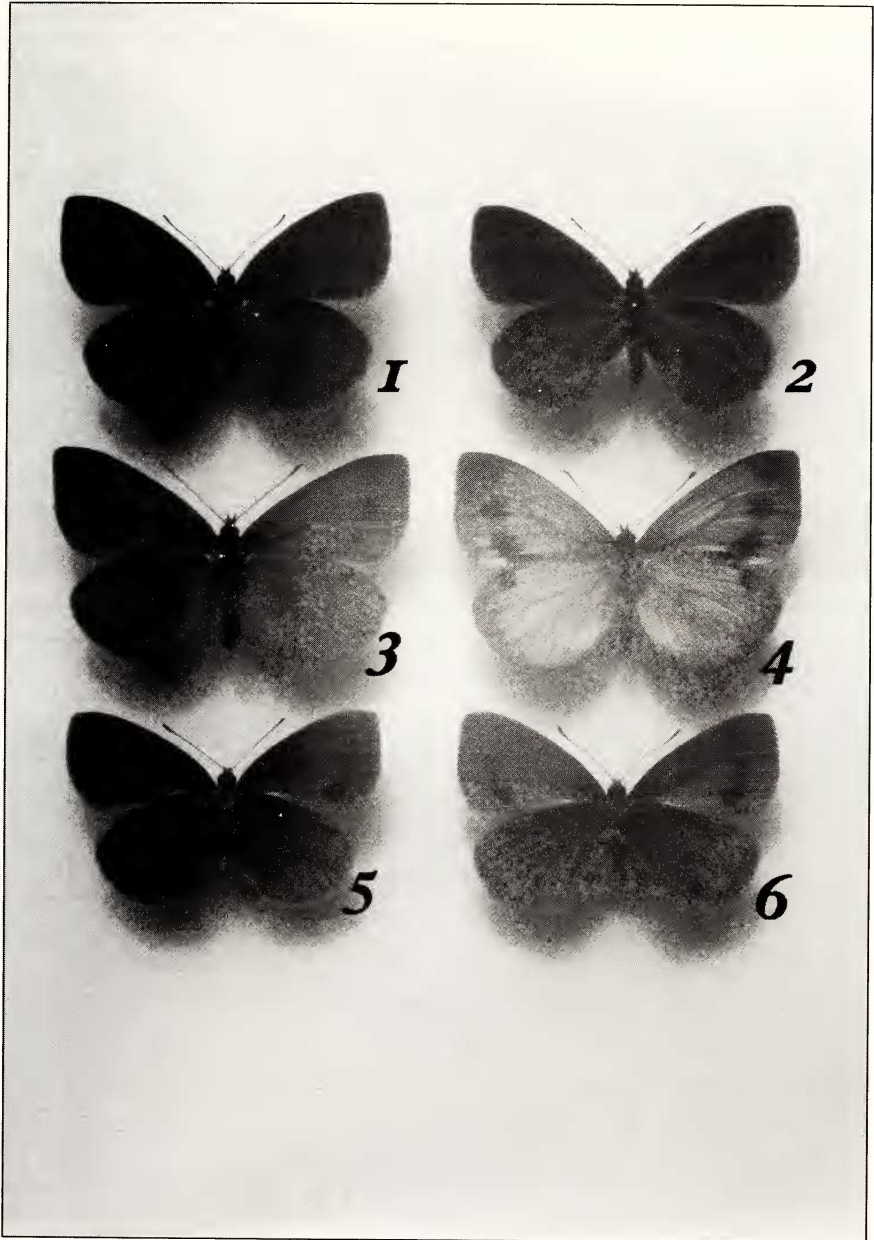


Plate C

(see page 58 for captions)